THE EFFECTS OF VARIOUS REMOVAL STRATEGIES ON FERAL HORSE POPULATIONS

A Report Submitted By:

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The following report describes the results of research conducted under P.O. YA530-PH9-786. The major objective of this contract was to investigate (primarily by means of computer simulation techniques) the effects of various strategies for removal of excess numbers of feral horses. Specific objectives, as described in the Statement of Work, were as follows:

1. Utilizing actual data from wild horse populations on public lands as supplied by the Bureau of Land Management (BLM), simulate via computer modeling the effects of various excess animal removal strategies concerning the following:
    a. effect of age-specific removals;
    b. effect of sex-specific removals.
2. Examine the effects of various strategies of fertility control on the rate of population growth and age structure.
3. Test for those population parameters which are most sensitive to producing population change.
4. Determine the sampling intensity that is needed to obtain a given degree of statistical precision in estimates of wild horse population parameters, e.g. recruitment and survival rates.

Recent papers by Nelson (1978), Wolfe (1980) and Conley (in press) contain the results of simulation studies similar to those conducted under this contract. Rather than merely duplicate the results of these investigations, an effort has been made to incorporate and build upon the pertinent findings thereof.

PROCEDURES

A series of population simulations were run by means of a computerized model of a modified Leslie matrix (Leslie 1945,1948). Detailed descriptions of the features and options of this program, developed by Dr. George S. Innis (1975), are given below and in the attached user's manual.

The input variables employed in the simulation runs were derived primarily from provisional estimates of various demographic parameters, based on an extensive analysis of unpublished BLM and USFS data from 18 feral horse populations in six states (vide Wolfe 1980, in press). These data were supplemented with those from more intensive investigations of individual populations in Montana (Feist and McCullough 1975) and northern New Mexico (Nelson 1978). In simulation trials that entailed age-specific fecundity rates, these values were derived from the results of an earlier investigation by Speelman et al. (1944) on the fertility of domestic horses raised under Western range conditions.

The initial population vector, employed in most of the simulations, consisted of 500 animals, apportioned among 19 age classes in an approximate geometric distribution. In simulation trials that involved male removals, the initial sex ratio was set at unity (i.e. 50:50); in other cases only the female segment was simulated. Unless otherwise specified, all simulations were run in a deterministic and density independent mode. Deviations from these procedures are explained below.

The results of the various simulation runs described herein are compared in terms of the finite rate of population increase (λ). In simple terms this value represents a measure of a given population's rate of increase, expressed as a ratio of the number of animals present in two successive years. In standard demographic notation this relationship is expressed as follows:

$$\lambda = \frac{N_{t+1}}{N_t}$$

where: N = numbers of animals
t = time (in years)

When λ is greater than 1.0, the population has increased in the time interval from t to t+1; when λ is less than 1.0, the population has decreased.

The finite rate of increase may also be considered as a growth multiplier (vide Rogers 1968). In a theoretical sense (see below) it is related to the conventional means of expressing annual rates of increase as follows:

$$\text{Percent increase} = (\lambda-1)(100)$$

Thus $\lambda=1.15$ is equivalent to an annual rate of increase of 15 percent. An initial population of 500 animals increasing at this rate for a period of 5 years would comprise 1,006 animals (i.e. 500 x λ^5, or 500 x 2.011) at the end of the fifth year. A more detailed discussion of the finite rate of increase can be found in Caughley (1977).

It is important to point out the limitations of the matrix approach to population analysis and, in particular, the restrictive assumptions associated with the use of the finite rate of increase to express population growth. Strictly speaking, λ is a hypothetical and assymptotic quantity that describes the growth rate that a population will assume only after a fixed schedule of age-specific birth and death rates have been operative in the population for a period of several years. That this condition represents an abstraction is obvious. However, for the purpose of comparing the potential effects of various removal strategies and the relative importance of various intrinsic population parameters, it constitutes a useful tool.

RESULTS AND DISCUSSION

Removal Strategies

As succintly identified by Caughley (1977:168), population management embraces three relatively distinct objectives:

1. treatment of a small or declining population to raise its density (i.e. conservation);
2. exploitation of a population to take from it a sustained yield; and
3. treatment of a population that is too dense, or which has an unacceptably high rate of increase, to stabilize or reduce its density (i.e. control).

With respect to feral horse populations on western rangelands, Nelson (1978:2) considered population management as an amalgamation of objective one, maintaining viable populations of feral horses, and objective three, limiting growth of local populations that reach pest proportions. In this context, it is essential to preface the following discussion of population management strategies with the distinction between removals that merely reduce the number of horses present in a given population and those, which actually depress or limit the future growth of the population (i.e. reduce the finite rate of increase below 1.0). Of the two, the latter strategy constitutes a more effective control measure.

Reduction of an existing population can be accomplished by means of one or a combination of two basic approaches. One method, sustained removal or continuous cropping, is aimed at maintaining the population at a reasonably constant numerical level. It involves the removal (usually on an annual basis) of a specified fraction of excess animals to balance increments to the population as the result of natality and immigration. Alternately, single or periodic removals of considerably greater magnitude may be executed to reduce the population down to a predetermined level, whereupon it is allowed to increase again over a period of several years. The use of the latter strategy has been proposed by DeByle (1979) for elk (Cervus elaphus) in areas where high densities are causing damage to forest regeneration.

Both strategies have advantages and shortcomings. The application of sustained removals presupposes reasonably accurate estimates of the levels of recruitment and natural mortality for the population in question. From an economic standpoint, the logistics involved in the removal of a small number of animals on a sustained basis are probably more costly than a single large-scale removal. However, the sociological ramifications of "boom and bust" management may render the latter strategy unacceptable. Moreover, if reproductive and survival rates in feral horse populations are subject to density-dependent influences, a drastic reduction of a given population could result in an acceleration in the annual rate of increase over that occurring prior to the reduction. The purpose of this report is not to discuss the socio-economic aspects of various removal strategies, but rather to analyze the demographic effects thereof.

Sustained Removals.-- Theoretically, sustained removals equivalent to a given average rate of increase should result in the maintenance of the population at a reasonably constant numerical level. Aside from methodological problems inherent in the determination of the "average" annual rate of increase and those associated with stochastic inter-annual variations in this parameter, this relationship is subject to semantic ambiguities in the the conventional means of expressing population growth rates. This can be shown by the following example.

Given a current population of 500 horses, increasing at a rate of 20 percent, the annual increment to the population will be 100 animals. It can be shown, however, that the removal of an equivalent number of individuals from the present population would result in a net deficit of 20 animals. The appropriate level of removal for the population in question would be equal to the projected increment divided by the predicted new population, or 100/600 = 16.7 percent of the existing population (i.e. 83 animals). The product of the residual population (417) and the finite rate of increase ($\lambda = 1.2$) will yield a new population of the same numerical strength as the original one. The balancing removal rate (BRR) can be expressed in more general terms as follows:

$$BRR = \frac{N_t - N_o}{N_t}$$

where: N_o = present population

N_t = projected new population (i.e. $N_o * \lambda$)

Note that if births constitute the only source of increment to the population in question, the BRR is equivalent to the percentage of young animals in the projected new population in the absence of any removals. A series of removal rates corresponding to the spectrum of values for annual rates of increase that may be encountered in feral horse populations is given in Table 1.

Table 1. Annual removals (percentages) required to maintain populations subject to varying rates of increase at a constant level.

	Finite rate of increase (λ)				
	1.05	1.10	1.15	1.20	1.25
Balancing removal rate (%)[a]	4.8	9.1	13.0	16.7	20.0

[a] BRR represents the fraction of the current population that should be removed to maintain a constant numerical level (see text for further explanation).

Given the relatively low rates of increase in feral horse populations in comparison to those of more fecund species, the comparatively small differences between the BRR values and rates of increase are largely an academic consideration, except where the rate of increase approaches biotic potential. Indeed, given the precision of present methods of estimating rates of increase, they are probably well within the range of sampling error that can be expected in such estimates. Only in situations, where the demographic unit is small (say less than 50 animals) and a slight but consistent degree of over-removal operates in conjunction with a series of random variations of fecundity and/or survival rates that are below the values that determine the mean rate of increase for the population in question, would the differences likely be of major consequence to the population.

Single Removals.-- Fig. 1 shows the results of several simulation runs, designed to illustrate the effects of various one-time removals ranging in magnitude from 10 to 90 percent of an initial population (in this case $N_o = 500$, $\lambda = 1.15$). The parallel lines represent population

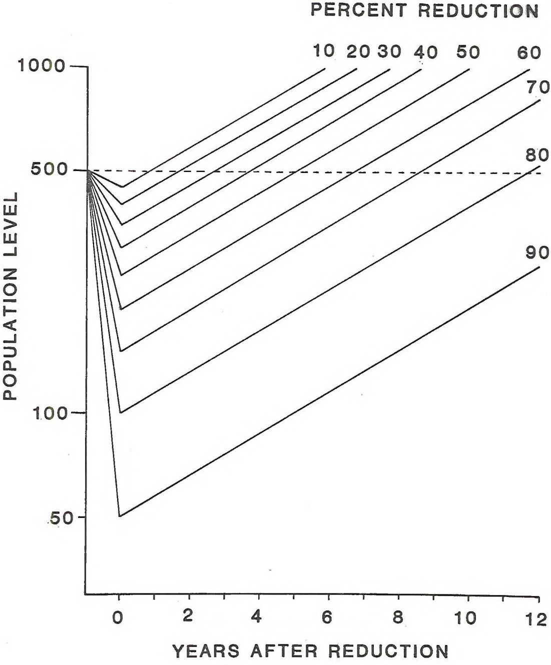

Fig. 1. Years required to reach initial population level following one-time reductions of varying magnitude for a population with a finite rate of increase (λ) of 1.15. The respective population levels are plotted on a semi-logarithmic scale.

levels in successive years following the reduction. A lambda value of 1.15 was chosen as being representative of a realistic upper limit for the rate of increase in feral horse populations throughout the western United States. The figure shows that, following reductions of 50 percent or less, the residual population will attain its original level in 5 years or less. Even in the case of reductions approaching total removal (i.e. 80-90 percent), the recovery period is only slightly more than a decade.

The slopes of the lines shown in Fig. 1 are a function of the rate of annual increase and will hold proportionately for any given initial population. A more comprehensive summary of the effects of single reductions is given in Table 2. The table shows the time (years) required for a population to equal or exceed its original level following one-time reductions of varying magnitude as a function of different increase rates. It will be noted that the only cases that might be considered as reasonably "permanent" reductions are those that involve drastic removals of populations with relatively low rates of increase. The data in Table 2 may be interpreted in another manner. Given a population that is increasing at a certain rate and the decision has been made that sustained annual removals do not constitute a feasible alternative, the values in the table may be used as a frame of reference to determine the magnitude of reduction required to keep the population from exceeding its present (or other predetermined) level for any desired time interval between successive reductions.

Age-specific Removals.-- Studies of other ungulates, such as white-tailed deer (_Odocoileus virginianus_) by McCullough (1979) and moose (_Alces alces_) by Lykke (1974), demonstrate that the manipulation of the

Table 2 . Years required for population to equal or exceed original level following a single (one-time) reduction of varying magnitude as a function of different rates of increase.

Percent Reduction	Finite rate of increase (λ)						
	1.08	1.10	1.12	1.14	1.16	1.18	1.20
10	2	2	1	1	1	1	1
20	3	3	2	2	2	2	2
30	5	4	4	3	3	3	2
40	7	6	5	4	4	4	3
50	9	8	7	6	5	5	4
60	12	10	9	7	7	7	6
70	16	13	11	10	9	8	7
80	21	17	15	13	11	10	9
90	30	25	21	18	16	14	13

Table 3. Effects of age-specific female removals on feral horse populations with varying rates of population increase.

Case (demographic parameters given below)[a]	Equivalent removal rates (%) and corresponding (λ) values				
	BRR (%)[b]	Foals only	Pre-reproductive (0-2 yr. olds)[c]	Primary-reproductive (3-9 yr. olds)	"Old age" (10+ years)
I (λ = 1.05)	4.8 (1.00)	24.0 (1.02)	9.6 (1.02	11.9 (0.98)	48.5 (1.00)
II (λ = 1.13)	11.4 (1.00)	64.2 (1.01)	21.8 (1.02)	42.6 (0.97)	____[d]
III (λ = 1.17)	14.3 (1.00)	82.7 (0.97)	34.0 (1.00)	41.1 (0.98)	____[d]

[a] Explanation of demographic parameters for various cases:

I: Survival rates (BSURV) for all age classes = 0.9; fecundity rates (BFECD) = values given by Speelman et al. (1944)

II: BSURV = 20*0.9; BFECD = 3*0, 17*0.5; minimum breeding age = 3 years

III: BSURV = 20*0.9; BFECD = 2*0, 18*0.5; minimum breeding age = 2 years

[b] BRR: no age-specific selectivity

[c] In case II removals included 3-year old animals

[d] In cases II and III this strategy was not possible because the population did not contain sufficient numbers of "old-age" females for an equivalent removal.

female age structure by means of age-selective harvest can be used to increase the maximum sustained yield (MSY) of the population. In essence, such a harvest strategy involves disproportionately greater removals among younger age classes, with the result that a greater fraction of older-- and presumably more fecund-- females remain in the population.

Conceivably, it should be possible to employ this strategy in reverse in the limitation of feral horse populations. Several simulations were run to test this hypothesis. To do this three hypothetical populations with differing rates of increase, obtained by varying fecundity schedules, were subjected to a series of annual age-specific removals. In all cases survival was held constant at 90 percent across all age classes. The removals in the various age segments were numerically equivalent to the BRR that would need to be applied across all age classes in order to stabilize the respective populations. Basically, the removal strategies were as follows: (1) removal of foals only; (2) removals limited to pre-reproductive age classes, including foals; (3) removals limited to the primary reproductive segment, i.e. age classes 3 or 4 to 9 years; and (4) removals limited to older age classes, i.e. 10-19 years.

In all but one case no provisions were made for age-specific differences in fecundity schedules between "old-age" animals and those in the primary reproductive segment. In the one case that incorporated age-specific fecundity rates, the values assigned were drawn from those given by Speelman et al. (1944) for domestic horses raised under range conditions.

The pertinent results of these simulation trials are presented in Table 3. In summary, the results indicate that only limited potential exists for manipulation of the rate of increase by means of age-specific female removals. Weighing the potential depression of the rate of increase (approximately 5 percent) against the problems involved in age determination in adult horses, the advantages to be gained by such a removal strategy appear minimal. This is probably attributable to the fact that the maximum potential production of young per reproductive female in equids is more or less genetically fixed at 1.0.

Sex-specific Removals.-- It is practically intuitive that a disparate sustained removal of females from a given population will effect a greater depression in the rate of population increase than the removal of an equivalent number of horses distributed equally over both sexes. For example, given a current population of 100 horses with an even sex ratio and a finite rate of increase of 1.10, the BRR is 9.1 percent or 9 horses from the total population. The removal of the same number of females would constitute approximately 18 percent of the female segment, which would be sufficient to effectively limit the growth of the population at virtually all levels of fecundity above 1.0 foals/breeding female (see Table 4).

Given the highly polygamous nature of horses, selective removals of males hardly appears to be a viable strategy of limiting the rate of population increase in feral horses. As has been amply demonstrated by management studies of other polygamous ungulates, male removals will reduce the absolute number of animals present in the population at any given time. In order, however, to effect any lasting reduction in the

Table 4. Finite rates of population increase (λ values) in feral horse populations as a function of various combinations of fecundity and survival.

Fecundity (foals/breeding female)[a]	Survival rate (%)						
	70	75	80	85	90	95	100
0.4	0.79	0.85	0.90	0.97	1.02	1.08	1.13
0.5	0.81	0.87	0.92	0.98	1.04	1.10	1.16
0.6	0.82	0.88	0.94	1.00	1.06	1.12	1.18
0.7	0.84	0.90	0.96	1.02	1.08	1.14	1.20
0.8	0.85	0.91	0.97	1.04	1.10	1.16	1.22
0.9	0.87	0.93	0.99	1.05	1.11	1.17	1.24
1.0	0.88	0.94	1.00	1.07	1.13	1.19	1.25

[a] Age at first breeding = 3 years.

rate of increase, a sufficient fraction of potentially breeding males must be removed on a sustained basis, so as to decrease the conception rate among reproductively mature females. The magnitude of such a sex-specific removal is determined by the number of females that can be effectively serviced by a single male of a given age class. The program used in these studies contains an option (FSBOM = females serviced by one male), which allows examination of the effects of this parameter.

Lacking reliable empirical data on the number of mares serviced by a single male, the results of the simulation trials conducted to test the effects of varying levels of male removals probably have limited meaning. It was arbitrarily assumed that male foals are physiologically incapable of effective breeding, and that yearling males could breed five mares each. All older males were assumed to service 20 mares. Thus FSBOM = 0,5,18*20. Obviously, these input data make no provision for behavioral patterns, which may modify the breeding potential of male horses.

Simulation runs were conducted to examine the effects of varying the levels of sustained non-age-specific male removals. The demographic conditions for the two cases simulated were as follows:

Case I: (λ with no removals = 1.07)
Fecundity (BFECD) = 2*0,0.25,17*0.6
Female survival (BSURV) = 0.8,19*0.9
Male survival (BSURVM) = 0.75,19*0.85
FSBOM = 0,5,18*20
Length of run (NRUNL) = 10 years

Case II: (λ with no removals = 1.11)
BFECD = 3*0,17*1.0
BSURV, BSURVM, FSBOM, NRUNL - same as in Case I

The results of these simulations indicated that sustained removals (over a 10-year period) approaching 50 percent of the male segment were necessary to effect any appreciable depression in the rate of increase.

By contrast, comparable results were obtained by application of sex-specific female removals of approximately 7 and 10 percent, respectively, for the two cases in question. Furthermore, the female removals resulted in an immediate depression of the rate of increase, whereas the male removals required a period of several years before the progressive distortion of the sex ratio produced a limitation in fecundity rates by the FSBOM function.

Effects of Fertility Control Measures

Permanent steriliation procedures applied to the breeding female segment are tantamount to a reduction of the fecundity rate. Examination of Table 4 provides some indication of the short-term effects of this strategy. For example, in a population with a female survival rate of 90 percent, the fecundity rate must be reduced to less than 0.4 foals per potentially reproducing female in order to achieve a "no-growth" condition. The actual degree of fertility control that must be applied to obtain such a condition will depend upon the fecundity rates that are operative in the population in the absence of any control measures.

Fertility control among females cannot be considered as a permanent solution to population limitation. Unless all females (including reproductively immature animals) are treated, recruitment of younger mares into the reproductive segment will eventually negate the effects of such measures. Since such a drastic strategy represents an impractical alternative, control measures must necessarily be implemented periodically. The interval between treatments will depend upon the intensity of a given control effort (i.e. the fraction of the breeding female segment rendered sterile).

Fertility control, induced by means of either temporary or permanent sterilization of dominant harem stallions, has been widely proposed as a technique for limiting the growth rate in feral horse populations. The appeal of such a technique is obvious, since in theory it requires treatment of only a small number of animals in a given population. Nelson (1978) investigated in detail the potential for use of this strategy and examined several behavioral requisites that must obtain for it to be effective. The primary assumptions are as follows: (1) only a fraction of the total male segment participates in the breeding; (2) this fraction is small relative to the pool of potentially reproducing females, such that many females are bred by a single stallion; (3) social groups are stable over time; and (4) if changes in band affiliation do occur, they involve primarily animals in the immature, pre-reproductive segment of the population.

The findings of Nelson's study indicated that the first two assumptions were met, but that contrary to the results of other studies of feral horse behavior (e.g. Feist and McCullough 1976) the premise of one male-many female reproductive units did not obtain. Nelson observed that a substantial fraction of the mature mares were involved in movements and reproductive activities outside their primary harem band. Furthermore, harem stallions were subject to an annual replacement rate of approximately 25 percent. Based on this evidence and the results of computer simulations, Nelson concluded that, even if the assumption of band fidelity was met, male-sterilization techniques would have to be implemented on an alternate-year basis, thus rendering this strategy impractical.

The present study afforded no opportunity to either corroborate or refute the validity of the behavioral observations in Nelson's analysis. It was, however, possible to replicate the population projections obtained by means of computer simulations in that study. Fig. 2 shows the results of a series of three simulation runs, designed to evaluate the effects of male fertility control measures under varying demographic conditions.

All cases presupposed the execution of a fertility control program, such that all dominant harem stallions were permanently sterilized at 5-year intervals over a time period (NRUNL) of 15 years. Cases I and II incorporated Nelson's estimate of the turnover rate among harem stallions of 25 percent per year, while Case III involved an estimated annual replacement rate of half of that value. The initial population level (ANUM = 500) was identical in all three cases. Likewise, survival rates were held constant at 90 percent for all cases and across all sex and age classes. Fecundity rates and corresponding λ values (in the absence of fertility control measures) for the respective cases were as follows:

Cases I and III: BFECD = 3*0,17*0.6; $\lambda = 1.06$

Case II: BFECD = 3*0,17*0.8; $\lambda = 1.10$

The results shown in Fig. 2 point out that the question of whether or not male fertility control measures can effectively limit the rate of increase in feral horse populations cannot be answered simply. The population response is subject not only to the behavioral constraints enumerated above, but also to intrinsic demographic parameters such as the survival and fecundity rates that are operative within a given population.

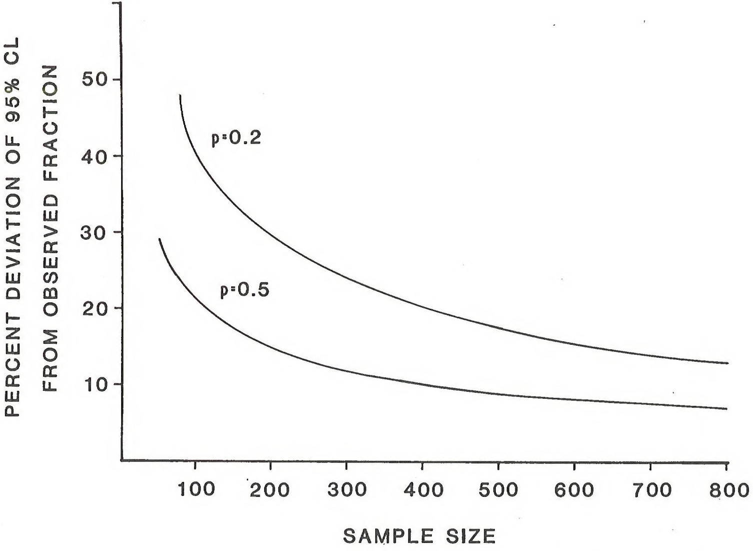

Fig. 5. Relationship of sample size to the percent deviation of the 95 percent confidence from the observed sample fractions for two probability functions (p = 0.2, and 0.5, respectively).

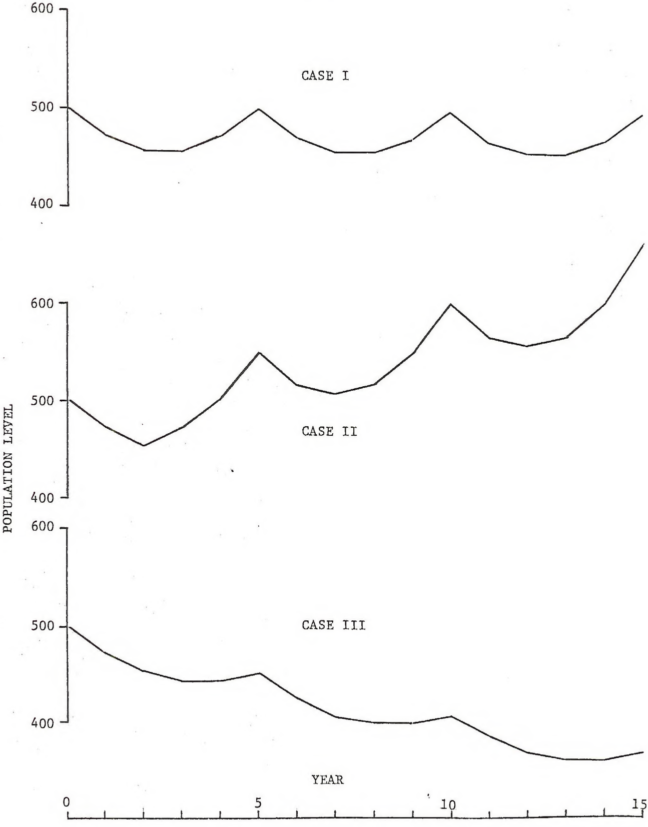

Fig. 2. Simulated responses of three hypothetical populations subjected to male-sterilization procedures at 5-year intervals. See text for explanation of various cases.

Sensitivity Analyses

As per Objective 3, several simulation trials were run to determine the relative sensitivity of various demographic parameters in terms of their effects on the rate of population change. The parameters examined were: (1) survival rate; (2) fecundity rate; (3) age at initial breeding; (4) maximum reproductive age attained by breeding females; and (5) breeding span (i.e. number of years that females in the population reproduce). The general approach employed here was to subject the parameter of interest to a range of values that reasonably can be expected to occur in feral horse populations, while holding the other parameters at constant levels.

A cautionary note should be interjected with respect to the interpretation of the results of these analyses given below. As Conley (in press) has pointed out, the rate of increase represents an integrative parameter that is influenced by all the component parameters enumerated above as well as the disparate effects of sex ratio, nutrition and density. To consider the effects of a single parameter-- thereby assuming no variation in the others-- does indeed represent an oversimplification. However, such an analysis has significant management implications; by determining the relative contributions of the various component parameters to the rate of population change, priorities can be established as to which of them should receive particular emphasis in data collection efforts.

Another limitation of this type of analysis is the fact that no provisions were made for age-specific variations in fecundity and survival rates. It is reasonable to expect that such variations do exist in free-ranging feral equid populations. For example, the mortality rate in the zero age class (i.e. among foals) probably exceeds that of adult animals, at least among young adults. Moreover, as appears to hold in the case of other large herbivores, male animals may be subject to higher mortality rates than females of comparable ages. To simulate all possible permutations and combinations of these values would, however, be virtually impossible and would cloud interpretation.

The above reservations notwithstanding, the results of these analyses identified survival and fecundity rates and age at first breeding as the primary determinants of population change. Table 4 summarizes rates of population increase as a function of various combinations of fecundity and survival. The values given in the table indicate an essentially linear response in the rate of population increase to changes in either parameter. Further examination of the table reveals that a given change in the survival rate generally effects a greater change in λ values than a comparable change in the fecudnity rate. For example, increasing the survival rate for all members of the population from 80 to 90 percent, while holding fecundity constant at 0.8 young per female of reproducing age, results in a 13 percent change in the rate of population increase. A comparable change in fecundity from 0.8 to 0.9, while holding survival constant at 80 percent, produces only a 2 percent change in the λ value.

The relationships between the rate of increase and the maximum age of reproductive females and the number of years that females remain in a reproductive condition (i.e. breeding span) are shown in Figs. 3 and 4, respectively. Both figures also illustrate the effects of varying female survival rates (BSURV) and Fig. 3 includes different minimum breeding ages (YCFRF). The curves in these figures further demonstrate the importance

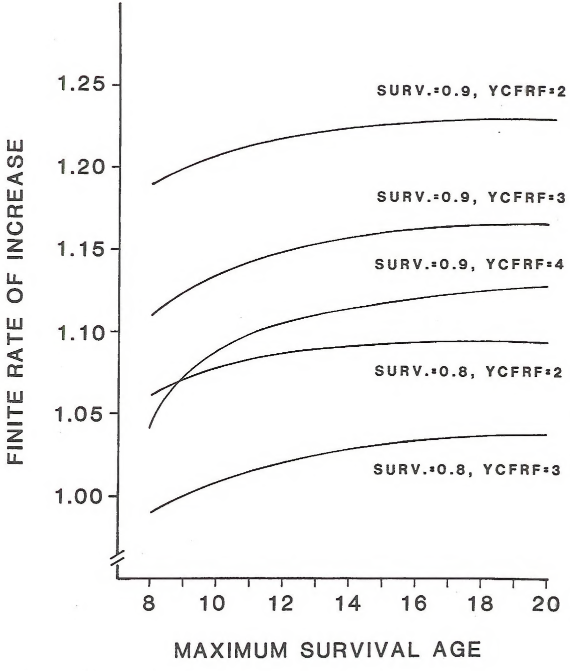

Fig. 3. Finite rates of increase (λ) obtained at various maximum ages and under differing combinations of female survival and initial breeding age (YCFRF).

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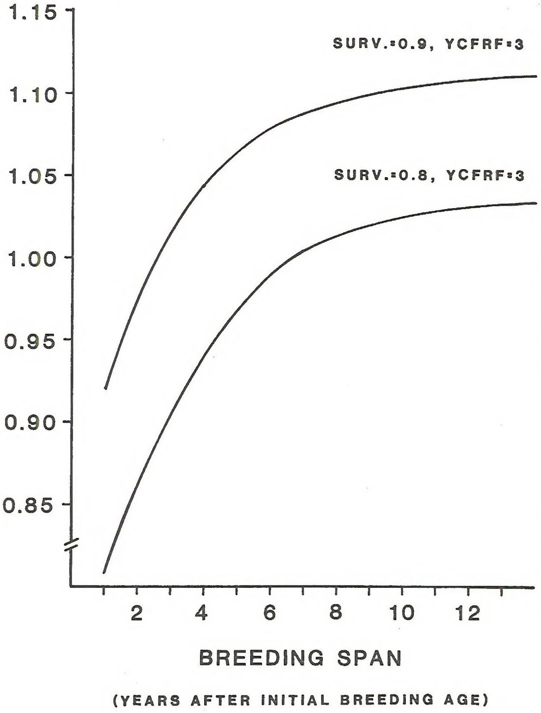


Fig. 4. Finite rates of increase (λ) obtained for various breeding spans (i.e. years after initial breeding) and under two schedules of female survival. The simulations were conducted assuming a reproductive rate of 1.0 foal/female for all females of ages 4 to x years.

of female survival and age at first breeding. For example, decreasing the minimum breeding age by 1 year, while holding the survival rate constant, results in an elevation of the finite rate of increase by approximately 4 to 7 percent. By contrast, as evidenced by the assymptotic shape of the curves, the former two attributes do not influence the rate of increase appreciably beyond some upper age threshold (say 12-14 years).

The results of the sensitivity analyses underscore the importance of obtaining reliable estimates of (1) survival rates (especially those of juveniles and young adults), and (2) reproductive performance in the primary breeding segment. Of particular significance is the relative proportion of reproducing females in the 2- and 3-year old age classes. On the other hand, and as Conley (in press) has pointed out, we can effectively ignore the maximum female survival age and the presence of post-reproductive females beyond approximately 14 years maximum age and 8 years of reproductive life, respectively.

Sampling Intensities (Objective 4)

As demonstrated above, reliable information on reproductive performance and/or recruitment constitute the most important requisite data inputs in determining the rate of increase in feral horse populations. Currently, composition counts of the sex and relative age structure (i.e. incidence of foals) constitute the most widely employed and economically feasible method of obtaining indices of productivity. In most cases, the data collected are expressed as an estimate of the percentage (or decimal fraction) of young animals in the total population. Since there exist only two possible outcomes-- young or adult-- data of this nature are usually considered to constitute a binomial distribution:

$$p + (1-p) = 1$$

where: p = fraction of foals in the population

Fig. 5 shows the 95 percent binomial confidence intervals, expressed as a percentage of the observed probability function, for two probability values at various sample sizes. Interpretation of the graphs proceeds in the following manner. If, for example, the observed incidence of foals in a sample of 100 animals from a given population were 20 percent (i.e. $p = 0.2$), the percent deviation of the 95 percent confidence interval from the observed fraction would be approximately 40 percent. In other words, at that level of sampling intensity one could expect the estimated fraction of foals in the population to be subject to a potential sampling error of approximately ± 40 percent. Even with drastically larger sample sizes, say approaching 800 animals, the precision of the observed fraction of foals would be only ± 15 percent.

Comparison of the two graphs in Fig. 5 also shows that the statistical precision of an observed fraction of $p=0.5$ is greater than that of $p=0.2$ over the entire range of sample sizes. The primary implication here is that some increase in the degree of precision for a given level of sampling effort may be obtained merely by expressing productivity indices in terms of the average number of young per female (i.e. foal:mare ratio), rather than as a fraction of the total population. Ideally, productivity should be expressed as the number of young produced per adult or potentially reproducing female. For example, if each adult mare produced a single foal, the probability function would be $p=0.5$ (1.0/1.0+1.0). Actually, such a reproductive level is unrealistic for free-ranging feral horses.

Available data from studies by Speelman et al. (1944), Feist and McCullough (1975) and Nelson (1978) suggest that only 40 to 60 percent of the reproductively mature mares actually produce foals each year. The approximate probability functions for this range of fecundity values fall between 0.3 and 0.4. For example, if each potentially reproducing mare produced an average of 0.5 foals per year, the corresponding probability function would be $p = 0.5/1.5 = 0.33$. Thus, the potential statistical precision of these probability functions for various sample sizes lie between the values given in the graph.

Under field conditions it is often difficult or impossible to distinguish between subadult and sexually mature females. Consequently, foal:mare ratios obtained from composition surveys may yield lower probability functions than those which express the number of foals simply as a fraction of potentially reproducing females. For example, in a hypothetical sample of 100 animals, that comprised 20 foals, 50 mares (including subadult animals), and 30 males, the probability function that expresses the foal:mare ratio would be $p = 20/70 = 0.29$.

Wolfe (1980) employed a technique, developed by Chapman and Robson (1960; see also Robson and Chapman 1961), to estimate survival rates in several populations. The method is can be used in the estimation of survival rates either from a time-specific sample of the age structure of a given population or from an analysis of successive recoveries of marked members of the population over time. The relationship of different sample sizes to the 95 percent confidence intervals of various estimated survival rates obtained by this technique is summarized in Table 5.

Table 5. Relationship of sample size to 95 percent confidence intervals of various estimated survival rates, obtained by the Chapman-Robson method[a].

Sample size	Estimated annual survival rate (s)				
	0.5	0.6	0.7	0.8	0.9
50	±.10	±.09	±.07	±.05	±.03
100	±.07	±.06	±.05	±.04	±.02
150	±.06	±.05	±.04	±.03	±.02
200	±.05	±.04	±.03	±.02	±.01

[a] Approximate confidence intervals obtained from the relationship:

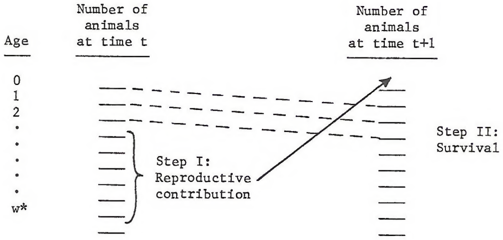
$$95\%\ CI = \pm(1.96)\sqrt{\frac{s(1-s)^2}{n}}$$

USER'S MANUALS

A copy of the LES User's Manual is appended to this report. The computer program described therein has been released for use by BLM personnel, but should not be distributed outside the agency except with written permission of its author (Dr. George S. Innis, Department of Wildlife Science, Utah State University, UMC 52, Logan, Utah 84322).

The user's manual is largely self explanatory. Users of the program not conversant with matrix models of population growth are referred to a very readable introduction to the topic given in Poole's (1974) text, An Introduction to Quantitative Ecology. As noted in the documentation, the original program was designed for simulations, in which the maximum number of age classes does not exceed 10. This limitation can be removed by minor changes in the dimension statements contained in the program. The listing and sample run of the program, included with this report, are for a modified version (EQUUS) of the original program, that will accommodate entry of age-specific input variables for as many as 20 age classes.

As noted in the user's manual, the iterative sequence involved in the projection of a population over time follows that of a conventional Leslie matrix. Briefly, the sequence is as follows: (1) the respective contributions of the reproducing age classes to the zero age class (foals) in the following year are computed; (2) the survival of animals in the various age classes from one year to the next is computed. Thus, the number of animals present in the population in the next consecutive year constitutes the summation of the the results obtained in steps 1 and 2. This sequence is diagrammed below.


Age
Number of animals at time t
Number of animals at time t+1
0
1
2
w*
Step I: Reproductive contribution
Step II: Survival

* w = maximum breeding age

In matrix notation this can be written as follows:

$$\begin{bmatrix} f_0 & f_1 & f_2 & f_3 & \cdots & f_{n-1} & f_n \\ S_0 & 0 & 0 & 0 & \cdots & 0 & 0 \\ 0 & S_1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & S_2 & 0 & \cdots & 0 & 0 \\ 0 & 0 & 0 & S_3 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & & & \vdots \\ 0 & 0 & 0 & 0 & \cdots & S_{n-1} & 0 \end{bmatrix}$$

where: f_x = age specific fecundity rates (number of young per female)

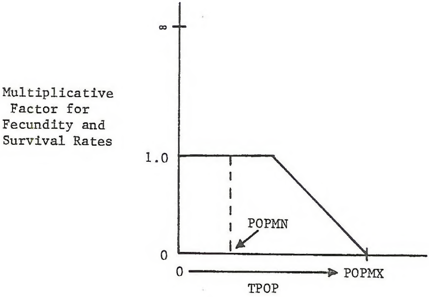
S_x = age specific survival rates

and n = number of age classes in the population

Obviously, this system is unrealistic for species such as feral horses with protracted gestation periods, during which some fraction of the reproducing females die and an unknown degree of intrauterine mortality occurs. The first problem (i.e. female mortality) is easily circumvented by multiplying the fecundity rates for each reproducing age class by the respective female survival rates. The products thus obtained ($\mathrm{BFECD}_x' = \mathrm{BFECD}_x * \mathrm{BSURV}_x$) are used as the input values for BFECD as described in the program documentation. In essence, this constitutes a modification of the original matrix described above. The modified matrix is given below:

$$\begin{bmatrix} f_0 S_0 & f_1 S_1 & f_2 S_2 & f_3 S_3 & \cdots & f_{n-1} S_{n-1} & f_n S_n \\ S_0 & 0 & 0 & 0 & \cdots & 0 & 0 \\ 0 & S_1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & S_2 & 0 & \cdots & 0 & 0 \\ 0 & 0 & 0 & S_3 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & 0 & 0 & \cdots & S_{n-1} & 0 \end{bmatrix}$$

Finally, a brief explanation to supplement that given in the user's manual regarding the program's density dependence option may be instructive. The diagram below shows the manner in which survival (BSURV and BSURVM) and fecundity (BFECD) rates are affected by varying population levels between zero and POPMX, if this option is invoked.



These functions may be tabulated in the form of a key as follows:

DDF ≠ -1

1. If TPOP ≤ POPMX/2, no effect.
2. If TPOP > POPMX/2, then survival and fecundity rates are decreased by a factor that varies linearly from 1.0 to 0.01.

DDF = -1

1. If POPMN = 0, no effect.
2. If TPOP ≥ POPMN, no effect.
3. If TPOP < POPMN, fecundity and survival rates are increased by a factor equal to $\frac{\text{POPMX}}{\text{TPOP} + 0.05}$

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